

# Life Cycles and Reproductive Strategies in Local Populations of *Rossiulus kessleri* (Lohmander) (Julidae, Diplopoda) from Isolated Habitats

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## ABSTRACT

Peculiarities of the postembryonic development and reproductive parameters in separate populations of *Rossiulus kessleri* Lohmander, 1926 were studied in two remote isolated forest habitats in the dry steppes of South Russia. Observations were carried out in a natural river-plain forest and shelter forest plantation differing in the edaphic and hydrothermal conditions. Seasonal rhythms of the development, duration of different stages, age and stage of the first reproduction in females, fecundity and natural mortality were considered in both populations. Patterns of the life-cycle of *Rossiulus kessleri* in secondary dry anthropogenic habitats seem to determine the following features of the reproductive strategy: delay in first reproduction and decrease of a total egg-production, which is compensated by low mortality rates in adult stages. Population differences in *Rossiulus kessleri* from isolated habitats are discussed in terms of K-selection and expansion capacity.

## RÉSUMÉ

Comparaison des cycles de vie et des stratégies de reproduction de populations locales de *Rossiulus kessleri* (Lohmander) (Julidae, Diplopoda) dans des habitats isolés.

Les modalités du développement post-embryonnaire et de la reproduction de populations séparées de *Rossiulus kessleri* Lohmander, ont été étudiées dans deux habitats forestiers isolés des steppes sèches du sud de la Russie. Les observations ont été effectuées dans une forêt naturelle de plaine et dans une plantation forestière protégée différant par leurs conditions édaphiques et hydrothermiques. Les rythmes saisonniers du développement, la durée des différents stades, l'âge et le stade de la maturation sexuelle des femelles, la fécondité et la mortalité naturelle ont été pris en compte dans les deux populations. Les modalités du cycle de vie de *Rossiulus kessleri* dans des habitats secs anthropisés semblent déterminer les paramètres des stratégies de reproduction - retard de la première reproduction et diminution de taille des pontes - qui sont compensés par un faible taux de mortalité des adultes. Les différences entre populations d'habitats isolés sont discutées en terme de sélection-K et d'augmentation de la capacité biotique.

## INTRODUCTION

Reproductive parameters and peculiarities of the postembryonic development have been studied in a number of diplopod species. These indices indicate variation in separate species and in separate populations of the same species from different geographical regions. For example, inter-population differences in the number of sexual and epimorphic stages of males have been recorded in *Bacillozonium nodulosum*, *Narceus annularis*, *Spelaeoglomeris doderoi* (SAHLI,

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1974). In different populations of *Schizophyllum sabulosum* the number of asexual stages during anamorphic development was found to vary from 3 to 5 (HALKKA, 1958; SAHLI, 1968, 1969). Interpopulation differences seem to be especially strongly expressed in species with polyzonal ranges, inhabiting sites with various edaphic and hydrothermic conditions.

The aim of this work was to compare the life-cycles and the reproductive indices in local isolated populations of *Rossiulus kessleri* from a river floodplain forest and shelter forest strips in the dry steppe subzone of Southern Russia.

*Rossiulus kessleri* is abundant in the forest-steppe and steppe zones of the European part of Russia. It usually predominates in diplopod communities of both natural and anthropogenic habitats (STRIGANOVA, 1977). These diplopods are well adapted to the climatic conditions of a steppe landscape with a hot and dry summer season. *Rossiulus kessleri* is often located in plots with tree and bush cover. Numerous aggregations of this species occurred in ravine and river plain forests and in wind protecting forest plantations (PRISHUTOVA, 1985; SIZOVA, 1985; STRIGANOVA, 1972; STRIGANOVA & PRISHUTOVA, 1990).

Extensive ploughed fields with a long-term monoculture of wheat are characteristic of this region of Russia. Plots with the natural tree and bush cover preserved and artificial forest strips represent isolated island habitats. The natural exchange between these forest islands seems to be impossible for non-flying invertebrates. The perennial isolation of separate populations of diplopods in island habitats suggests the possibility of the existence of different microevolutionary trends in populations living in diverse ecological situations.

#### SITES AND METHODS

Materials for this study were collected in Rostov and Stavropol regions in two sites being 30-40 km apart:

1. River flood-plain forest of one of the Don tributaries two species dominated: *Salix alba*, *Alnus glutinosa*. Soil was grey sandy river-plain soil. Litter layer was a constant, 7-10 cm depth, grass cover under a closed tree canopy.

2. 30-year old shelter forest strip in a watershed position. Predominate tree species: *Fraxinus excelsior*, *Robinia pseudoacacia*, *Populus nigra*. Soil - typical chernozem of the loamy texture. Litter layer was 23 cm depth, completely decomposed by June. Grasses covered about 70 % of the ground under the canopy.

The habitats differed significantly in the hydrothermic regime of the upper soil horizons. Soil humidity in the river-plain forest was constantly high, due to the high level of ground water. A high relative humidity at aboveground level was maintained by a dense grass cover. Dry leaf litter dried out only in mid-summer during a drought.

The forest plantation was situated in the zone of an unstable moisture. The litter and soil dried out in summer and the relative humidity of the upper horizon ranged between 5-12 %.

Quantitative samples of diplopods were taken twice per month in both plots from April to October. Diplopods were collected by a hand-sorting from standard quadrats (25 x 25 cm, depth 10 cm).

The live body mass, sex and developmental stage were determined in all specimens sampled. Mature females were dissected to record the presence of eggs.

Periods of the spring moulting, oviposition, presence of juveniles and start of the winter diapause were recorded. The post-embryonic development (longevity of separate stages, growth of the body mass and mortality) was studied in the laboratory.

Eggs obtained from females kept into laboratory jars were placed in Petri dishes. Both longitudinal and transversal diameters of eggs were measured to compare egg sizes from different populations. Larvae that hatched from eggs in the laboratory were reared in groups in jars with soil and leaf litter taken from their natural habitats.

#### RESULTS

The spring moult of *Rossiulus kessleri* in the river-plain was observed in late April. Diplopods moulted in the soil and did not build moulting chambers. Oviposition was completed in May, and in the mid-June pupoids were recorded in experimental clutches.

In the forest plantation the spring moulting was delayed by 10-15 days. Almost the diplopods built moulting chambers what was observed in both the natural habitat and laboratory). Females began to oviposit in late June, and young larvae appeared in July-August. During dry years the oviposition was delayed until autumn.



The stadium of 1st oviposition differed in separate populations: X - in the river-plain and XI - in the forest plantation. Relative numbers of egg-laying females increased in progressively older stadia (Fig. 1). The percentage of egg-laying females increased in stages X-XII in the river-plain from 56 to 100%. In the forest plantation the percentage of egg-laying females was much lower in all reproductive stages and increased from 19% to 81%.

Mature females showed differences in body mass and fecundity (Figs 2, 3). An increase in the fecundity of older stadia has been recorded in other diplopod species - *Cylindroiulus latestriatus*, *C. punctatus*, *Julus scandinavicus* (BAKER, 1978; BLOWER, 1970). The relationship between body mass and fecundity has been described in *Ommatoiulus moreleti*, *Julus scandinavicus* and *Glomeris marginata* (HEATH, BOCK & MOUNTFORD, 1974). The multiple correlation between the developmental stage, body mass and fecundity has been calculated for both populations of *R. kessleri* under study (PRISHUTOVA & MINORANSKY, 1984). The correlation coefficients averaged 0.91 - for the river-plain and 0.80 - for the forest plantation. Figure 3 shows that the smaller females of the stage XII from the river-plain have a higher fecundity than bigger females of the same stage from the forest plantation.

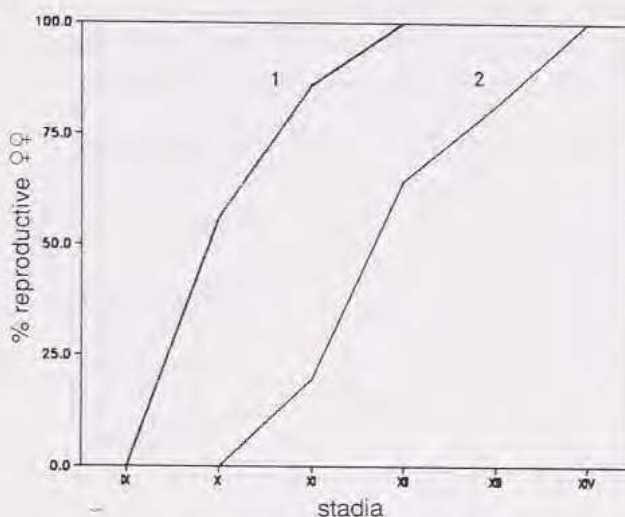


FIG. 1. — Relative number of reproductive females (%) in the older stadia of the development. 1: river-plain forest (n=98); 2: wind protecting forest plantation (n=113).

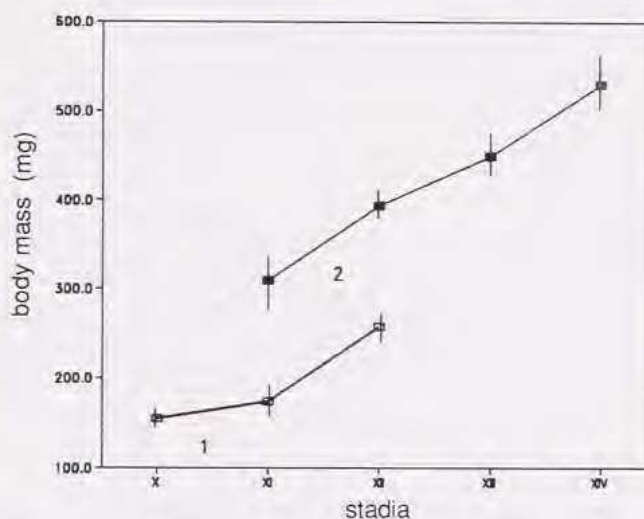


FIG. 2. — Body mass of mature females (mg) in the older stadia of the development. The bars represent one standart error of the mean. 1: river-plain forest (n=98); 2: wind protecting forest plantation (n=113).

TABLE 1. — Total volume (mkl) of the egg production in females of different stages from separate populations of *R. kessleri*.

| Stadia             | X      | XI     | XII    | XIII   | XIV     |
|--------------------|--------|--------|--------|--------|---------|
| River-plain forest | 34.969 | 37.587 | 58.157 |        |         |
| Forest plantation  | -      | 61.446 | 67.683 | 76.923 | 104.874 |



Egg sizes had clear interpopulation differences: river-plain: longitudinal diameter (mm)  $0.826 \pm 0.03$  and transversal diameter (mm)  $0.658 \pm 0.03$ ; forest plantation: longitudinal diameter (mm)  $0.860 \pm 0.03$  and transversal diameter (mm)  $0.714 \pm 0.01$  ( $P = 0.001$ )

(PRISHUTOVA, 1985). The mean egg volumes were calculated approximating their form to an ellipsoid. Individual mean volume of eggs from the river-plain averaged 0.187 mkl and that from the forest plantation 0.231 mkl. Table 1 shows the total volume of egg production in females of different stages from both populations.

The relationship between the mean mass of reproductive females and the total volume of their egg-production is shown by Figure 4. Correlation coefficients between these indices averaged 0.99 and 0.94 for the population from the river-plain and forest plantation respectively. The correlation for the whole range of female biomass values was not found to be significant.

Duration of individual stadia was different for each population. Figure 5. shows the rates of the development for stadia II-VII in the laboratory. The total duration of these stages averaged 115 days in the river-plain population and 100 days in the forest plantation one. Significant differences ( $P \leq 0.05$ ) were observed in stadium VII only, and these were apparently related to differences in sex differentiation. Sex differentiation begins in stadium VII in the river-plain population, and stadium VIII in the forest plantation population.

Rates of post-embryonic development under favourable laboratory conditions were evidently higher than in natural habitats, as revealed by parallel field samples. But the growth of body mass progressed slowly. Mass of individual diplopods in natural habitats was 1.5-2 times as high

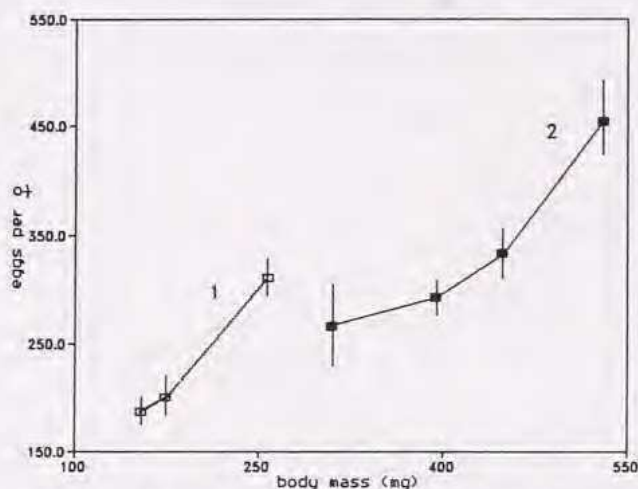


FIG. 3. — Fecundity vs. body mass in mature females.  $\bar{x} \pm SE$ . 1 & 2 as in Figure 1.

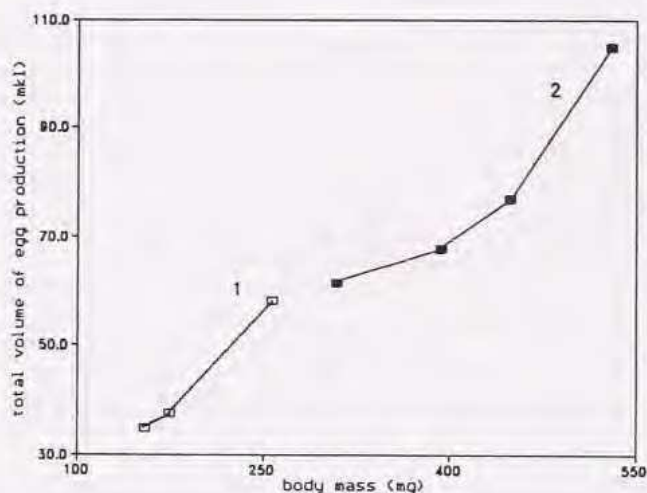


FIG. 4. — Relationship between the mean body mass of reproductive females and the total volume of their egg production. 1 & 2 as in Figure 1.

as that in laboratory specimens of the same stadia.

In the river plain, *R. kessleri* reached V-VIII during the first summer, IX-X the next year, and the 1st reproduction took place during the third year. Individuals of stadium XIV were recorded in this population. The minimum duration of the life-span is 4-5 years.

A mass emergence of young larvae in the forest plantation was observed in August. All larvae built moulting chambers near the soil surface. 10-15 individuals were found in one



chamber. Before a winter diapause they reached III-IV, in the second year - VIII-IX and in the third - X-XI. The first reproduction took place in the fourth year of life. This population had 15 post-embryonic stages. The total life-span is 5-6 years - a year longer than that in the river-plain. During unfavourable years, the number of egg-laying females remained relatively low and did not exceed 40% of the total amount laid by mature females. This seems to be the reason why the life-span of this population can be prolonged to 8 years.

The mortality dynamics were studied under laboratory conditions (Fig. 6). In the river-plain, maximum mortality rates were recorded in adult stages, which reproduced at least once. In the forest plantation a significant increase in natural mortality was observed during the sexual differentiation. These features, together with the differences of seasonal rhythms affect the population structure.

Figure 7 presents the population structure in both habitats during two subsequent years as stadia recorded from soil samples. The bulk of the population in the river-plain was represented by reproductive stadia. The relative importance of the stadium IX increased in autumn because of the recruitment from the younger generation. In different seasons all stadia were present in the population. The seasonal changes in the age composition in both years were similar.

In the forest plantation the pre-reproductive stadium X predominated in the first spring. Older mature were absent. In autumn, stages XI-XII predominated and single specimens of older stadia appeared. The following spring all adult stadia were present, but VIII-X together barely exceeded 10%. Their mass increased slightly by the following autumn. Replacement rates of generations were delayed by a year in the forest plantation, in comparison with those in the river-plain population.

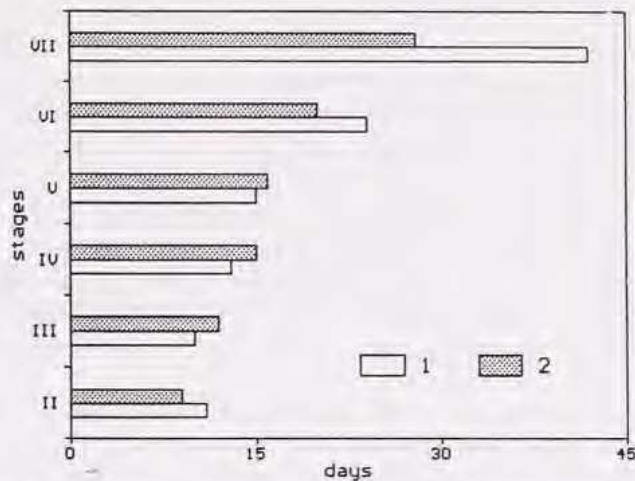


FIG. 5. — Development rates of stadia II-VII in the laboratory for individuals of the river-plain population (1) and of the forest plantation population (2).

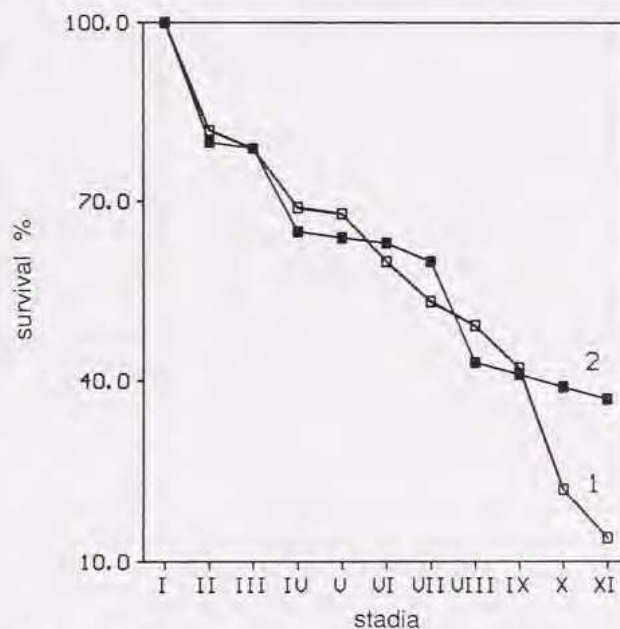


FIG. 6. — Mortality dynamics studied under laboratory conditions for individuals of the river-plain population (1) and of the forest plantation population (2).

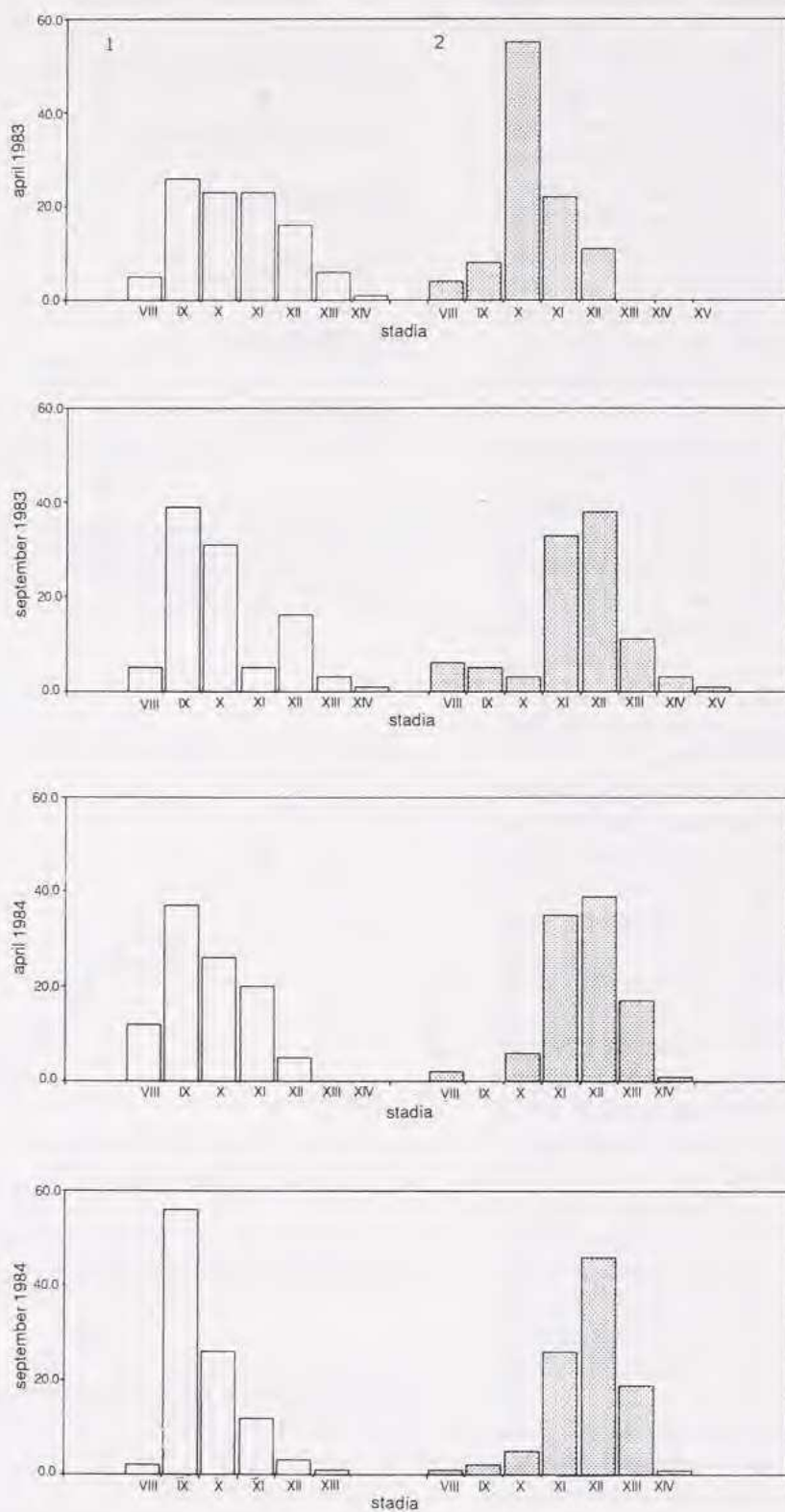


FIG. 7. — Population structure during two subsequent years: river-plain population (1); forest plantation population (2).



## DISCUSSION

The analysis of the population structure, the reproduction tactics and the development rates of *R. kessleri* in isolated habitats revealed clear interpopulation differences in the life-cycle. A long summer drought in the soil of an artificial forest plantation promotes a long aestivation period for all stadia. The timing and duration of the summer pause was found to depend on weather conditions in distinct years. The juvenile were particularly susceptible to the hydrothermic conditions. They ceased to feed at the elevated soil temperature even under high moisture levels, while adults continued the normal feeding activity (STRIGANOVA, 1972).

Diplopods living in dried out habitats have to accumulate energy reserves for a summer aestivation, which minimizes the energy quota for reproduction. Accumulation of energy reserves results in the increase in body mass in all stadia, which was observed in diplopods from the forest plantation, in comparison with those from the river-plain (PRISHUTOVA, 1985). The delay in first reproduction can be also interpreted in terms of the energy allocation within the population.

In addition, diplopods from the forest plantation have significant energy expenses for the building of moulting chambers. This building activity was recorded in all stadia. The activity of larvae of the first stadia seems to be provided by a nutrient supply in the eggs. The eggs in these populations were bigger than those from the river-plain populations.

Numerous julid species use to present typical K-selection features such as perennial life-cycle, iteroparity, fixed seasonal rhythms, large body mass etc. (cf. PIANKA, 1970). All these features are characteristics of *Rossiulus kessleri*.

*Rossiulus kessleri* has 7 asexual stadia. This is the maximum number recorded in Julidae (SAHLI, 1969, 1974). Interpopulation differences in the duration of separate larval stages are insignificant, depending more on the longevity of inactive periods, than on those of an active growth.

The number of sexual stadia shows the inter-population differences (2 - in the river plain and 3 - in the forest plantation). The same was shown in separate populations of *C. teutonicus* (SAHLI, 1969).

Discussion of the factors determining the time of first reproduction considers two alternatives - genetic determination of an age or of a stadium of first reproduction (DAVID, 1992). The results here are consistent with the idea of the stadia as the main determinant. Under unfavorable conditions, for example during heat deficiency, diplopods reach their genetically fixed stadium of maturity at an older age, as described in high mountains (MEYER, 1985).

Interpopulation differences in the stadium of first reproduction can be considered as a result of the micro-evolutionary processes. Populations of *R. kessleri* under study differed in both stage and age of the first reproduction. Age can vary between individuals within the same population, for example in the forest plantation only 18% of females reaching stadium XI participated in reproduction. Hence, age appears to be a more resilient population feature, depending on local conditions.

An acceleration of maturation is associated with a restriction of life-span, as shown, for example, in *Nemasoma varicorne* (BROOKES, 1974). Populations of *R. kessleri* showed the same relationship. The shorter life-span was characteristic of diplopods from the more favourable natural habitat (river plain forest), which can be considered the primary biotope for *R. kessleri* in steppes. The artificial forest plantations represented the secondary habitats populated by these diplopods. The prolongation of the life-cycle and the delay in first reproduction seem to be adaptations to unfavourable anthropogenic habitats.

The prolongation of the life-span to account for long inactive periods is characteristic of many poikilotherms under extreme conditions. K-selection features allow diplopods to select these tactics. The development of this evolutionary trend was recorded only in stable populations capable of increasing their accumulated reproduction reserve with aging, and of continuing an



active growth between reproductive cycles (STEARNS, 1976). These traits are characteristic of *R. kessleri*. This is why this species is so widely distributed in dry steppes where it occurs in both natural and anthropogenic habitats. Life-cycle traits are obligatory population features, they were recorded under both field and laboratory conditions and can be considered as phenotypical features.

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